

CLASSIFICATION AND EVOLUTION OF THE BRACHIOPOD FAMILY RUGOSOCHONETIDAE MUIR-WOOD 1962

By N. W. ARCHBOLD

Department of Geology, University of Melbourne, Parkville, Victoria 3052

ABSTRACT: The Rugosochonetidae are reclassified into six subfamilies namely: Rugosochonetinae Muir-Wood 1962, Pliochonetinae Sokolskaya 1960, Undulellinae Cooper & Grant 1975, Lamellosiinae Cooper & Grant 1975, Quinquenellinae Archbold 1981 and Svalbardiinae subfam. nov. The Chonetinellinae Muir-Wood 1962 should be allowed to lapse. Phylogeny of the Rugosochonetidae is discussed and its geographic distribution and possible migration routes are also documented.

The brachiopod family Rugosochonetidae, with a history spanning some 160 million years from the Middle Devonian until the end of the Permian, became the most diverse (generic level) family of the Chonetidina during the Carboniferous and maintained this dominance in Permian brachiopod faunas (Afanasyeva 1975a, 1978a). At present, the family includes 29 genera with 19 having been identified since the major studies of Sokolskaya (1960) and Muir-Wood (1962).

Elevation of the Rugosochonetinae Muir-Wood (1962) to family status (Cooper & Grant 1975) is justified because of the change in scope and content of the family. Nevertheless, considerations of the content and phylogeny of the family indicate the necessity of modifying the existing sub-familial classification. The scheme discussed below differs substantially from that given by Cooper & Grant (1975) whose review was restricted to North American Permian genera.

For this review the summary papers on Carboniferous and Permian chonetaceans by Afanasyeva (1975a, 1978a) have been an invaluable compilation of data on the ranges and distributions of rugosochonetid genera. As a result the discussions herein on generic distributions and migrations are supplementary to those papers, and supply necessary corrections and more recent information. The terminology applied to the Rugosochonetidae is that used by Archbold (1981e).

TAXONOMIC CRITERIA

Cooper (1970) demonstrated the value of the dorsal internal structures of articulate brachiopods for generic and higher levels of classification of the phylum and hence it is not surprising that the Rugosochonetidae was defined by Cooper & Grant (1975) on those structures. However, dorsal internal structures of the Chonetidina change through ontogeny (Greene 1908, Sokolskaya 1949) and therefore analysis of genera should be based on large collections.

Sokolskaya (1946) stressed external ornament in distinguishing stocks of chonetids, a character also used by Cooper & Grant (1975) in their classification of subfamilies within the Rugosochonetidae. Many members of the Rugosochonetidae lack true radial ornament but the dorsal valve of most smooth genera is pseudocapillate when worn which reflects the distribution of

fine radiating taleolae, the long axis of which is parallel to, rather than normal to, the exterior surface of the valve. These fine taleolae, which occur just below the thin primary layer of the dorsal valve, are found in all members of the Undulellinae, Lamellosiinae and the majority, if not all, of the Svalbardiinae subfam. nov. I consider pseudocapillate ornament to be a significant taxonomic criterion within the Rugosochonetidae.

PROPOSED CLASSIFICATION

Suborder CHONETIDINA Muir-Wood 1955

Superfamily CHONETACEA Bronn 1862

Family RUGOSOCHONETIDAE Muir-Wood 1962

Subfamily RUGOSOCHONETINAE Muir-Wood 1962

GENERA INCLUDED: *Rugosochonetes* Sokolskaya 1950 (= *Nix* Easton 1962); *Waagenites* Paeckelmann 1930 (= *Dienerella* Reed 1931); *Mesolobus* Dunbar & Condra 1932; *Chonetinella* Ramsbottom 1952; *Neochonetes* Muir-Wood 1962; *Arctochonetes* Ivanova 1968; *Schistochonetes* Roberts 1971; *Paramesolobus* Afanasyeva 1975; *Jakutochonetes* Afanasyeva 1977; *Dagnachonetes* Afanasyeva 1978; *Tenuichonetes* Jing & Hu 1978.

Subfamily PLIOCHONETINAE Sokolskaya 1960

GENERA INCLUDED: *Plicochonetes* Paeckelmann 1930; *Striatochonetes* Mikryukov 1968; *Rugaria* Cooper & Grant 1969.

Subfamily SVALBARDIINAE subfam. nov.

GENERA INCLUDED: *Svalbardia* Barkhatova 1970; *Lissochonetes* Dunbar & Condra 1932; *Dyoros* Stehli 1954; *Quadrochonetes* Stehli 1954; *Eolissochonetes* Hoare 1960; *Sulcataria* Cooper & Grant 1969; *Chonetinetes* Cooper & Grant 1969; *Komiella* Barkhatova 1970; *Capillonia* Waterhouse 1973; *Leurosina* Cooper & Grant 1975; *Leiochonetes* Roberts 1976.

Subfamily UNDULELLINAE Cooper & Grant 1975

GENERA INCLUDED: *Undulella* Cooper & Grant 1969; *Micraphelia* Cooper & Grant 1969.

Subfamily LAMELLOSIINAE Cooper & Grant 1975

GENERA INCLUDED: *Lamellosia* Cooper & Grant 1975.

Subfamily QUINQUENELLINAE Archbold 1981

GENERA INCLUDED: *Quinquenella* Waterhouse 1975.

DISCUSSION AND DIAGNOSIS FOR PROPOSED CLASSIFICATION

Family RUGOSOCHONETIDAE Muir-Wood 1962

(nom. trans. Cooper & Grant 1975, p. 1212 ex. Rugosochonetinae Muir-Wood 1962, pp. 32, 64.)

AMENDED DIAGNOSIS: Small to medium sized, costate, capillate, smooth or lamellose chonetaceans. Dorsal interior with pronounced lateral septa, long median septum and deep alveolus. Cardinal process externally quadrilobed and internally bilobed; it may be externally bilobed in early members of the family. Ventral sulcus absent to strongly developed; median septum of variable length, high posteriorly; hinge spines oblique to nearly vertical. Pseudodeltidium and chilidium may be present.

DISCUSSION: Cooper & Grant (1975) raised the taxon from sub-family to family status but did not provide a diagnosis although it is clear from their comments (Cooper & Grant 1975, p. 1212) that the family was recognised on the basis of internal structures, especially the nature of the cardinal process.

The family Rugosochonetidae contains a diverse group of genera united by common internal dorsal features. Six subfamilies can usefully be recognised at present.

Subfamily RUGOSOCHONETINAE Muir-Wood 1962

AMENDED DIAGNOSIS: Small to large sized rugosochonetids with radially capillate or costate external ornament. Ventral sulcus feebly to strongly developed. Hinge spines at low to moderate angle. Dorsal fold present in several genera; brachial ridges often well developed.

DISCUSSION: The Rugosochonetinae is restricted to include only those genera with an external ornament varying from capillate to costate. The Chonetinellinae Muir-Wood (1962) is permitted to lapse. Muir-Wood (1962) assigned three genera to that subfamily: *Neochonetes*, *Chonetinella* and *Waagenites*. The first was reassigned to the Rugosochonetinae by Cooper & Grant (1975). *Chonetinella* is a broadly interpreted genus (Grant 1976) and includes species which approach Western Australian Permian species of *Neochonetes* (Archbold 1981c). *Waagenites* is still poorly known, its dorsal interior never having been adequately illustrated, and is provisionally assigned to the Rugosochonetinae. At present the genus is broadly interpreted (Waterhouse & Piyasin 1970, Grant 1976) and includes species with poorly developed sulci. The Chonetinellinae as characterised by Cooper & Grant (1975), grouped together rugosochonetids with a distinct sulcus. They also included *Chonetinetes* Cooper & Grant (1969) within the subfamily because of that genus being similar in gross morphology to *Chonetinella*. To group chonetid genera together on the basis of the presence of a prominent sulcus is a dubious criterion; the development of heterochronous, homeomorphic ventral sulci in different stocks of chonetaceans has previously been discussed by Archbold (1980a). *Chonetinetes* is provisionally assigned herein to the *Svalbardinae* subfam. nov.

Discussion of remaining rugosochonetids is restricted to poorly understood genera. The variable external ornament of *Mesolobus* has been extensively discussed by many authors. Hoare (1960) demonstrated that North American, early Pennsylvanian species are capillate while younger species are smooth. The type species, from high in the Pennsylvanian, was considered by Weller & McGehee (1933) and King (1965) to be smooth, whereas Girty (1915) and Dunbar & Condra (1932) agreed with Norwood & Pratten (1855) in considering the species to be capillate. The query remains; how smooth are the smooth species? Girty (1915, p. 63) noted that "when large series of specimens from different horizons are examined, individuals more or less intermediate in character are found. That is, associated with the smooth variety are a few shells which show faint, yet unmistakable traces of radial sculpture". Sutherland & Harlow (1973) showed that even smooth species of *Mesolobus* occasionally show faint capillae commonly near the anterior margin. Following Dunbar & Condra (1932) the ornament of *Mesolobus* is considered to be finely capillate, at times "obsolescent".

Arctochonetes Ifanova (1968) is assigned to the Rugosochonetinae. The bifurcating ventral median septum of *Arctochonetes* appears to be a stronger development of the short median septum and pair of ridges on either side of the adductor muscle field of *Neochonetes*.

A new genus belonging to the Rugosochonetinae (Fig. 1) is typified by *Neochonetes unbonoplicatus*, from the Sakmarian Nenets Beds, Sula River, Northern Timan Mountains, as figured by Barkhatova (1964). The ventral valve is capillate, possesses a distinct, posteriorly developed sulcus which changes anteriorly to a swollen fold, separated from the lateral flanks of the valve by a valley on either side. The species has not been formally described and hence is a *nomen nudum*, but rather than describe the new species and genus here, on the basis of the only figured specimen, description is left to those with access to a collection of specimens so that the ontogeny of the ventral valve can be fully assessed.

Subfamily PLICOCCHONETINAE Sokolskaya 1960

AMENDED DIAGNOSIS: Small, strongly convex capillate to costate rugosochonetids. Hinge spines oblique to high angle. Fold and sulcus absent. Interior generalised, often poorly known.

DISCUSSION: Although not adopted by Muir-Wood (1962), this subfamily was redefined and reconstituted by Cooper & Grant (1975). The subfamily still appears to include a heterogeneous group of genera and further work is required to define the scope of the subfamily. *Plicochonetes* appears morphologically far removed from *Dagnachonetes*, regarded herein as the ancestral rugosochonetid, and this suggests that the Rugosochonetidae may be polyphyletic. Muir-Wood (1962) showed that the hinge spines of *Plicochonetes* are slightly curved and extended at a high angle to the hinge. *Sriatochonetes* Mikryukov (1968), a finely costellate genus with high angle hinge spines, is inadequately known internally and hence is provisionally included in

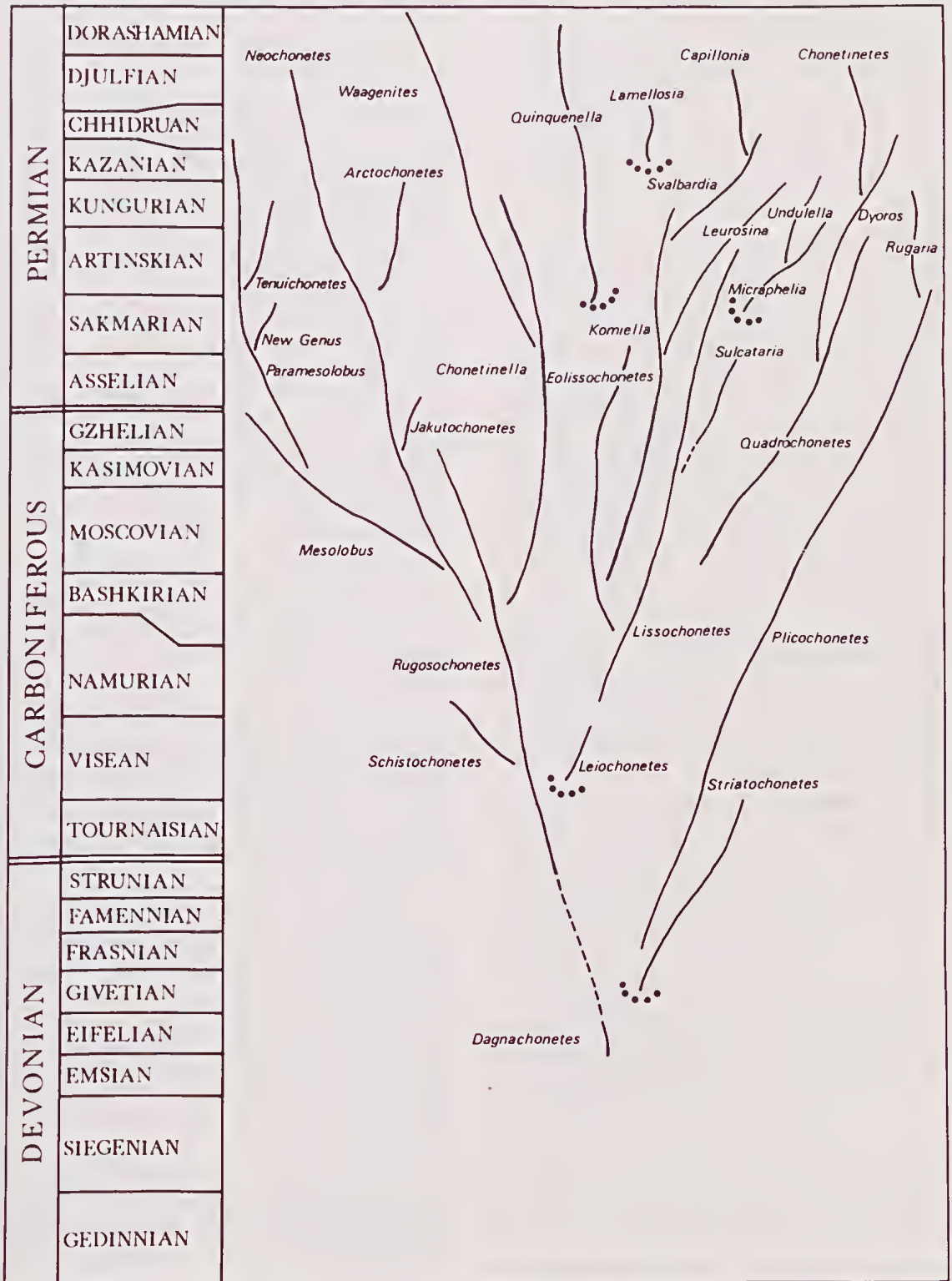


Fig. 1—The inferred phylogeny of the Rugosochonetidae Muir-Wood showing the relationship of the constituent genera. Subfamilies are separated by curved, dotted lines.

the Plicochonetinae following Mikryukov (1968). The type species, *Strophomena setigera* Hall 1843, well figured externally by Hall (1843, 1862), possesses hinge spines at a high angle which may indicate a relationship for the genus with either the Strophochonetinae or the Retichonetinae, both of the Chonetidae, although it does not preclude the genus from the Rugosochonetinae. *Rugaria* Cooper & Grant (1969), with oblique hinge spines, was well described by its authors and is interpreted herein as a direct descendant of *Plicochonetes*.

Subfamily SVALBARDIINAE subfam. nov.

DIAGNOSIS: Small to medium sized, externally smooth rugosochonetids. Dorsal exterior pseudocapillate when worn. Hinge spines at low to moderate angle.

DISCUSSION: Members of this subfamily are distinguished from the Quinquenellinae by the absence of accessory septa and the presence of dorsal pseudocapillae when worn, and the Undulellinae by the possession of hinge spines at a much lower angle to the hinge. The Undulellinae are also characterised by pronounced development of the brachial ridges and subtle variations in the arrangement of the dorsal septa. Probably all the constituent genera of the Svalbardiinae possess the distinctive taleolate shell structure which results in a pseudocapillate shell ornament, especially of the dorsal valve when the shell is worn. This is considered to be a unifying feature of this stock of the Rugosochonetidae and is shared with the Undulellinae and the Lamellosiinae. Confirmation of the pseudocapillate ornament is required for the dorsal valves of *Quadrochonetes* and *Leiochonetes*. Pseudocapillate shell structure may be noted for the following genera as figured and/or discussed by the various authors:

Lissochonetes Dunbar & Condra (1932, p. 171, pl. 20, fig. 48)

Sulcataria Cooper & Grant (1975, pl. 478, fig. 62)

Dyoros Stehli 1954, Cooper & Grant (1975, pl. 481, fig. 10, pl. 485, figs 12, 13; subgenus *Lissosia* Cooper & Grant 1975, pl. 487, fig. 18; subgenus *Tetragonetes* Cooper & Grant 1975, pl. 489, figs 26, 32 and pl. 490, fig. 72)

Chonetinetes Cooper & Grant (1975, pl. 477, figs 2, 49)

Lenrosina Cooper & Grant (1975, pl. 495, fig. 3)

Komiella Barkhatova 1970, Liehew (1934, pp. 12, 100)

Capillonia Waterhouse 1973 (see Waterhouse 1964, pl. 3, figs 1, 10 as discussed by Archbold 1981b)

Svalbardia Barkhatova, as discussed by Archbold (1981b)

Chonetinetes and *Dyoros* both possess a pseudocapillate ventral valve as well as dorsal valve suggesting a close relationship for the two genera.

Eolissochonetes Hoare 1960 is stated to possess "no trace of true radial striation" (my italics). A hint of a pseudocapillate ornament is shown for *Quadrochonetes* Stehli by Cooper & Grant (1975, pl. 502, fig. 17).

The shell structure of *Leiochonetes* Roberts (1976) is not known but Roberts' description indicates a comparable feature may be present.

Following Brunton (1972) I consider that the microstructure of the brachiopod shell is important to systematics. The distinctive shell structure in the Svalbardiinae, Undulellinae and Lamellosiinae, possibly reflecting the positions of setae along the mantle edge, just below the primary layer of the shell, which were differentially filled with shelly material, structurally different to that of the remainder of the secondary layer, appears to unite the three subfamilies closely. Similar shell structure has not been noted for true capillate rugosochonetids which, when worn, are smooth.

Lissochonetes, despite good illustrations of the type specimens by Geinitz (1867) and Mudge & Yochelson (1962) and discussions by Dunbar & Condra (1932), Muir-Wood (1962) and Cooper & Grant (1975), remains poorly known. It should be restricted to weakly sulcate species with delicate dorsal internal structures until large collections are available. *Komiella*, with stout lateral septa and a long median septum fused anteriorly of a deep alveolus (Archbold 1981b), appears useful for separating species from the ill-defined *Lissochonetes*. The type species of *Komiella*, of Kazanian age, has been recorded from as early as the Middle Carboniferous (Afanas'yeva 1977) indicating that the genus spans a considerable time interval.

Subfamily UNDULELLINAE Cooper & Grant 1975

AMENDED DIAGNOSIS: Small smooth rugosochonetids. Exterior of dorsal valve pseudocapillate when worn. Hinge spines at high angle (nearly 90° to the hinge). Brachial ridges and dorsal median septum prominent; cardinal process small.

DISCUSSION: The Undulellinae are morphologically close to the Svalbardiinae, being distinguished from that subfamily by details of the hinge spines and dorsal interior. The pseudocapillate appearance of the dorsal valve when worn is added to the subfamilial diagnosis, in order to emphasise the relationship of the Undulellinae to the Svalbardiinae.

Subfamily LAMELLOSIINAE Cooper & Grant 1975

AMENDED DIAGNOSIS: Concentrically lamellose rugosochonetids with no radial ornament. Pseudocapillate shell when worn.

DISCUSSION: I follow Cooper & Grant (1975) and include this subfamily in the Rugosochonetidae, but as the dorsal interior is unknown, the familial assignment is only tentative. Support for the rugosochonetid affinities of *Lamellosia* comes from the pseudocapillate nature of the shell when worn.

Subfamily QUINQUENELLINAE Archbold 1981

AMENDED DIAGNOSIS: Small, smooth rugosochonetids, not pseudocapillate when worn. Dorsal interior with short lateral septa, long accessory septa and a variably developed median septum.

DISCUSSION: The development of long accessory septa and the lack of a pseudocapillate dorsal valve when worn sets this subfamily apart from other smooth

rugosochonetids. Phylogenetic implications of the lack of pseudocapillae are discussed below.

PHYLOGENY OF THE RUGOSOCHONETIDAE

INTRODUCTION

The inferred phylogeny of the Rugosochonetidae is shown in Fig. 1.

While it is beyond the scope of the present review to discuss fully the applicability of particular stage names in subdividing the Carboniferous and Permian Periods, it should be noted that several of the subdivisions in Fig. 1 are provisional and serve merely as a guide to time control for the development of the family.

The problem of the relationship of the Gzhelian and Asselian Stages, especially with respect to the "Orenburgian" stage, has been reviewed by Waterhouse (1978a). The view that much of the Orenburgian is basal Asselian is strongly indicated by the re-examination of the classic brachiopod faunas, and a review of other fossil groups, of the Samara Bend by Prokof'ev (1975), who maintained that the Gzhelian is the youngest stage of the Carboniferous, a view consistent with the most recent monographic study of the Carboniferous of Fergana (Sikstell *et al.* 1975).

The Chhidruan as used herein equals the Punjabi of Stepanov (1973) and Waterhouse (1976). Use of the name Punjabi is avoided because of the earlier informal use of the same name by Reed (1936, 1939) for early Permian faunas of the Salt Range.

The phylogeny diagram is dendritic in style. Diverging branchlets do not necessarily imply that two genera or subfamilies become less similar to each other through time. Several genera appear to result from small changes to the ancestral genus; e.g. *Neochonetes* from *Rugosochonetes* (Archbold 1981e). Other genera appear abruptly with no obvious antecedent (e.g. *Quadrochonetes*) as do the two subfamilies, Lamellosiinae and Quinquenellinae. No scale of variation is intended by the curved branchlets although genera do not exhibit a constant morphology, but rather show changes in morphology from species to species. These trends will not be in a constant direction—as might be inferred from straight lines. A species may show a constant morphology (reflecting a constant gene pool); a genus, of more than one species, never will. Diverging branchlets may be interpreted from Fig. 1 to imply divergent evolution of two genera although, as stated above this is not necessarily the case.

Variations in the external gross morphology of the shell from genus to genus within chonetacean families such as the strength of the sulcus is probably related to environmental factors, such as the nature of the substrate. The development of heterochronous homeomorphs occurred in different families and subfamilies (Archbold 1980a).

The ancestry of the Rugosochonetidae is likely to lie within the Chonetidae. The Parachonetinae of Johnson (1970) appear an ideal group to be the ancestor of the Rugosochonetidae because of the similarity of the

dorsal internal structures of the two groups. *Parachonetes*, common in Emsian age rocks (Johnson 1970), is a suitable ancestor for the Rugosochonetinae. It seems likely that the Rugosochonetidae is polyphyletic in origin, but it appears possible, judging from illustrations of *Parachonetes* by Johnson (1966, 1970) that the Plicochonetinae and the Rugosochonetinae may have both arisen independently from the Parachonetinae by modification of the external ornament and convexity of the ventral valve. The earliest member of the Rugosochonetidae appears to be the Eastern European, Eifelian genus *Dagnachonetes* which possesses a simplified, bilobed cardinal process (Afanas'yeva 1978b) but the derivation of the Plicochonetinae from *Dagnachonetes* appears unlikely. *Striatochonetes*, appearing in the Givetian, may not belong to the Plicochonetinae and is certainly far removed morphologically from *Dagnachonetes* and yet both genera are close in time. Similarly the origin of the small, highly convex Frasnian genus *Plicochonetes* is obscure and appears distinct from *Dagnachonetes*. *Plicochonetes* has a substantial time range if the referral of the Artinskian *Plicochonetes minor* to the genus is correct (Ting 1965). *Rugaria* was probably derived from *Plicochonetes* by modification of the hinge spines and cardinal process.

EVOLUTION OF THE RUGOSOCHONETIDAE

The Rugosochonetidae first appear in the Eifelian, and then reappear in the earliest Carboniferous with the genus *Rugosochonetes*. *Rugosochonetes* has a substantial time range and early species of *Neochonetes* are similar to species of *Rugosochonetes*. The local development of *Schistochonetes* in northwestern Australia, from *Rugosochonetes* occurred in the Viséan by modification of the external ornament (Roberts 1971). *Neochonetes* arose from *Rugosochonetes* in the Bashkirian, or a little earlier, and various stocks subsequently developed within the genus (Archbold 1981e). *Jakutochonetes* appears to have been a local development, in northeastern USSR, from *Neochonetes* during the Late Carboniferous by slight modification of the sulcus and fold (Afanas'yeva 1977). *Arctochonetes*, by modification of the ventral median septum, developed from a *Neochonetes* ancestor in the Artinskian.

Mesolobus (Sutherland & Harlow 1973) is most closely related to *Neochonetes* and probably evolved from that genus in the early Moscovian. Hoare (1960) considered that *Eolissochonetes* evolved from *Mesolobus* but *Eolissochonetes* has been shown to be older than *Mesolobus* (Afanas'yeva 1975a, Hoare *et al.* 1979). In the late Pennsylvanian, members of *Mesolobus* with an obsolescent ornament died out in North America but in the Kasimovian of the Moscow Basin *Paramesolobus*, with a stronger radial ornament flourished (Ivanov & Ivanova 1936, Afanas'yeva 1975b) and has been widely recorded from the Late Carboniferous of southern Europe including Spain (Winkler-Prins 1968, 1970), and the Karnic Alps (Schellwein 1892, Heritsch 1931, Vinassa de Regny & Gortani 1905). Species of *Paramesolobus* are usually poorly known but an

approximate assessment of the Permian range of the genus can be made from illustrated accounts of chonetids usually referred to either of Schellwein's species *Chonetes sinuosa* or *Chonetes latesinuata*. *Paramesolobus* is known from the Asselian-Sakmarian of Thailand (Yanagida 1967), Japan (Nakamura 1959, Tazawa 1976), Spitzbergen (Gobbett 1964, pl. 15, fig. 10) and the Karni Alps (in the form of *Chonetes* sp. nov. Heritsch 1938). It has been reported from the Artinskian of the Karakorum (Renz 1940) and the Kungurian of China, in the form of *Chonetes plicatiformis* Chan & Lee (1962). Younger Permian forms have been described by Coogan (1960) from California (a form with weaker capillae), by Cooper & Grant (1975) from Texas, in the form of *Mesolobus? permianus* and a Chhidruan form is known from Japan (Hayasaka 1925, pl. 5, figs 5, 6). Cooper & Grant (1975) considered that *Mesolobus? permianus* represented a convergence towards *Mesolobus*, but the Texan occurrence can be explained as a descendant species of *Paramesolobus*. The new genus, discussed above within the Rugosochonetinae, was apparently derived from the *Paramesolobus* stock during the Sakmarian by modification of the fold and sulus. *Tenuichonetes* may have evolved from either *Mesolobus* or *Paramesolobus* during the Artinskian.

Chonetinella evolved during the Bashkirian, possibly from the same stock of *Rugosochonetes* that gave rise to *Neochonetes*, by the development of a distinct sulus and fold. The origin of *Waagenites* is obscure. The earliest species, from the Sakmarian of the Urals, is *Chonetes (Dienerella) fasciger* Mirskaya *et al.* (1956) which possesses the characteristic deep sulus and very coarse costae of the genus. *Waagenites fasciger* has invariably been overlooked by subsequent authors who have assumed that *Waagenites speciosus* from the late Artinskian or Kungurian of Thailand was the earliest species of the genus. Waterhouse & Piyasin (1970) and Grant (1976) noted that *Waagenites speciosus* was very different from *Waagenites grandicosta* (Waagen) the type species of the genus. Muir-Wood (1962) was not able to elucidate all the dorsal internal structures of *Waagenites* but she did indicate that the dorsal interior was unlike that of *Neochonetes*. Grant (1976) stated that the dorsal interior possessed short lateral septa, and a short median septum, low and near the valve centre, but unfortunately he did not figure any of his topotypes and from his diagnosis one cannot determine the precise relationship of the three dorsal septa. It appears that *W. speciosus* does not belong in *Waagenites* s.s. Illustrations of the species by Grant (1976) and Yanagida (1971) revealed that the ventral sulcus (strongly developed in the ancestral and type species of the genus) is weakly developed or even absent in the Thai species. Two comments can be offered regarding the taxonomic position of *Waagenites speciosus*. Firstly, the dorsal interior structures of *W. grandicosta* (Waagen) require full description and need to be figured. Secondly, the present author agrees with Yanagida (1971) who considered that the species is close to *Neochonetes* in details of mor-

phology of the shell and dorsal internal structures. Nevertheless the relatively coarse costellae of the Thai species would result in a modification of the generic diagnosis of *Neochonetes* in order to accommodate the species in that genus. A new generic name is probably required for the species, the new genus being a development from a neochonetid stock. Huang (1932) described and Liao (1980) recorded several species of "*Chonetes*" or "*Waagenites*" from the Late Permian of Kweichow, China, some specimens of which are large, coarsely costate and possess a weak sulus and hence they are possibly descendants from the Thai species. *Waagenites* is a generic name that should be applied with caution until the type species is well understood. The evidence of Mirskaya *et al.* (1956) strongly suggests that the genus already possessed a well developed, deep sulus in the Sakmarian and hence reports of the genus from the Chhidruan of Primorya (Licharew & Kotlyar 1978) and Japan (Tazawa 1976) also require re-examination.

The Svalbardiinae first appeared with *Leiochonetes* during the middle Visian in New South Wales, although Roberts (1976) discussed two other poorly known Early Carboniferous occurrences of smooth chonetaceans that may be allied. *Leiochonetes* is a small, unspecialised smooth rugosochonetid and hence is an ideal ancestor for the group. *Leiochonetes* which possibly does not possess a pseudocapillate dorsal valve or a similar genus, may also have independently given rise to the Quinquenellinae by modification of the dorsal septa (Archbold 1981a). Two principal lineages may be delimited within the Svalbardiinae.

The *Dyoros* lineage, appearing in the Kasimovian with *Quadrochonetes*, is characterised by the development of a pronounced ventral sulus. Arising from *Quadrochonetes* in the late Sakmarian, *Dyoros* became a major element of Texan Permian chonetacean faunas (Cooper & Grant 1975). *Dyoros* possesses prominent dorsal septa and this trend appears to have been accentuated by the development of *Chonetinetes* with a modified elevated cardinal process. The dorsal septal arrangement of *Chonetinetes* is consistent with an origin for the genus from *Dyoros*. The ancestry of *Quadrochonetes* is not well understood as the genus possibly lacks pseudocapillate shell structure which suggests an origin from *Leiochonetes* or an unknown ancestor. *Dyoros* and *Chonetinetes* are unusual for the Svalbardiinae in that they both possess pseudocapillate shell structure of both valves.

The *Svalbardia* lineage represents a broader, more varied development with subgroupings, although relationships are obscured because of uncertainty over the internal morphology of *Lissochonetes*. Accepting the diagnosis of *Lissochonetes* given by Muir-Wood (1962, p. 77), it appears possible to derive *Sulcataria* from *Lissochonetes* as *Sulcataria* also possesses poorly developed lateral septa with a more prominent, posteriorly placed, dorsal median septum. Species of *Lissochonetes* and *Sulcataria* are generally small.

Eolissochonetes possibly evolved from *Lissochonetes* by modification of the lateral septa and pro-

duction of a long thin median septum. However, early species of *Eolissochonetes* are close to representatives of *Komiella* and both genera appeared at about the same time. The earliest species of *Lissochonetes* is *Lissochonetes montinis* (McKellar 1965) occurring as early as the late Visean (Roberts 1975) and probably the species evolved directly from *Leiochonetes*. *Lissochonetes montinis* has a dorsal septal arrangement similar to that in *Eolissochonetes morsei* (Hoare *et al.* 1979) and is also similar to species assigned to *Lissochonetes* from the Late Carboniferous of Kazakhstan by Sokolskaya (1968) and the Late Carboniferous Magarsk Horizon of the Gizhiga River Basin by Afanas'yeva (1977) that would now be assigned to *Komiella*. Younger species of *Eolissochonetes* (Hoare 1960, 1961) exhibit the distinctive internal morphology of the genus and are larger. *Komiella* may be derived from early species of *Eolissochonetes* or both genera may be derived directly from early species of *Lissochonetes*.

Leurosina is internally similar to *Komiella* suggesting derivation from that genus; it differs in anterior curvature of the ventral valve and the prominent raised anterior recurved portions of the brachial ridges (Cooper & Grant 1975, pl. 479, fig. 78). The latter feature also occurs in *Svalbardia* and *Capillonia*. *Svalbardia* possesses short hinge spines while the younger and larger *Capillonia* possesses long delicate hinge spines.

The two representatives of the *Undulellinae* are morphologically close to the *Svalbardiinae*, differing only in details of the hinge spines and the dorsal interior, and hence the *Undulellinae* can be derived from the *Svalbardiinae*, probably from an unspecialised "*Lissochonetes*" or perhaps *Leurosina*. The origin of the *Lamellosiinae* is obscure but the pseudocapillate shell structure of *Lamellosia* suggests an origin within the *Svalbardiinae*.

MIGRATIONS AND ENDEMISM

With the origin of the family in eastern Europe, the descendant genus, *Rugosochonetes*, attained a cosmopolitan distribution during the Carboniferous. One descendent of *Rugosochonetes* namely *Schistochonetes* remained a localised endemic development in northwestern Australia while another, *Neochonetes*, attained a wide distribution in the Permian. *Mesolobus* reveals endemic development and then extinction in the North American Pennsylvanian, with a re-introduction of the descendent, essentially European genus *Paramesolobus* into Japan and North America in the Late Permian. *Chonetinella* has been reported widely from the Late Carboniferous and Early Permian but it appears premature to determine stocks within the genus and possible migration effects. *Waagenites* appeared in the Early Permian as a rare element in the Ural seas, later spreading its range to the Tethys, including the Caucasus (Licharew 1936), the Salt Range, Pakistan (Waagen 1894, Reed 1944), the Himalaya (Waterhouse & Gupta 1979) and Burma (Diener 1911). *Jakutochonetes* is an endemic development in the Late Car-

boniferous of the Kolyma-Omolon region of the USSR, while *Arctochonetes* is restricted to the Artinskian of the Boreal region of the USSR.

The *Svalbardiinae* appeared in eastern Australia in the Visean and became widely distributed by the Late Carboniferous. *Lissochonetes* and/or *Komiella* had penetrated North America, Kazakhstan, northeastern USSR, European USSR (Ivanov & Ivanova 1936), Spain (Winkler-Prins 1968) and South America (Amos 1960, Mendes 1959) by the Late Carboniferous. Endemic development took place in North America in the Late Carboniferous with the development of *Quadrochonetes*. During the early Permian, endemic development of the *Quadrochonetes* stock continued in North America with the development of the genus *Dyoros* which subsequently penetrated the Boreal sea in the Late Artinskian and Kungurian (Ivanova 1968, 1972). Solomina (1978, p. 106, pl. 9, fig. 3) recorded, with some question, the possible occurrence of *Dyoros* in the Late Carboniferous Khaldan Suite from the Southern Orulgan region of northeastern USSR. Her specimens are inadequate for precise determination, nevertheless, the illustration indicates a strongly sulcate form that may be a species of *Quadrochonetes* or *Dyoros*. *Dyoros* entered northern Gondwana waters during the Chhiduran in the form of ?*Sulcataria pentagonalis* (Waterhouse 1978b, Waterhouse & Gupta 1979). *Sulcataria* and *Leurosina* appear to be endemic developments of the *Svalbardiinae* in North America. *Svalbardia* exhibits a bipolar or disjunct distribution in the Kungurian (Archbold 1981b), while *Capillonia* is restricted to the Kazanian and younger Permian of New Zealand (Waterhouse 1973) and eastern Australia in the form of *Lissochonetes semicircularis solida* (Dear 1971).

The *Undulellinae* are restricted to the Permian of North America as are the *Lamellosiinae*. The *Quinquenellinae* exhibit a bipolar or disjunct distribution in the Permian, being found in Western Australia, the Himalaya, possibly south-east Asia and northeastern USSR (Archbold 1981a). The occurrences of *Paramesolobus*, *Dyoros* and *Rugaria* on both sides of the Pacific at times during the Permian indicate some potential for migration between the two regions by several rugosochonetid genera.

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